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LIFE HISTORY ASPECTS OF THE TIGER SALAMANDER (*AMBYSTOMA TIGRINUM MAVORTIUM*) IN THE CHIHUAHUAN DESERT

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An isolated population of tiger salamanders (*Ambystoma tigrinum mavortium*) was most intensively studied from September 1962 through the spring of 1967, but periodic observations were made as late as the spring of 1969. Whitford and Sherman (1968), Whitford and Massey (1970), and one of us (Webb, 1969) previously discussed some information pertaining to this population of salamanders.

For financial assistance in the academic years 1962-1963 and 1963-1964 (grants to Webb), we are grateful to the University of Texas at El Paso University Research Institute. For aid in the field, we are indebted to James R. Dixon, Robert M. Kinniburgh, Jo Ann Brown, Artie L. Metcalf, R. Roy Johnson, H. Ellison Rodgers, Arthur J. Ward, Edward M. Stern, and Richard C. Lovelace. We are grateful to Richard D. Worthington for comments concerning the manuscript. All measurements refer to total length. Gehlbach (1967) summarized pertinent literature for the species.

Study Area and Habitat

Since permanent water is lacking in the area, cattle interests have necessitated the construction of numerous artificial ponds. Tiger salamanders were studied in one of these cattle tanks or ponds which, along with an adjacent windmill and large water-storage tank, is locally known as Taylor Well. It is located in an extensive north-south trending tract of the Chihuahuan Desert known as the Jornada del Muerto, and it is within the confines of the Jornada Experimental Range. Taylor Well, about 4,400 ft elevation, is approximately 19 miles north-northeast of Las Cruces, Doña Ana County, New Mexico, between the Doña Ana Mountains to the west and the San Andres Mountains to the east (Fig. 1). The average annual rainfall is about nine inches and the average annual temperature about 14.5 C.

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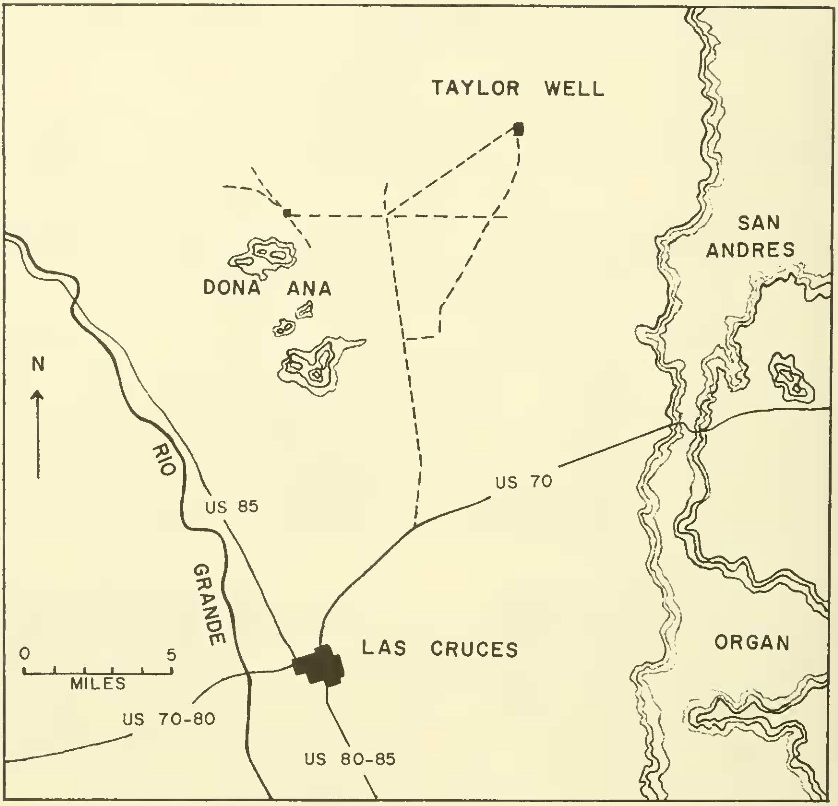

Fig. 1. Map of Las Cruces and vicinity, Doña Ana County, New Mexico, showing mountain ranges, Rio Grande, and location of Taylor Well; all dirt roads in area (dotted lines) not shown.

The desert terrain in the vicinity of Taylor Well is flat and supports a sparse, shrubby vegetational cover on loose sandy or hard-packed clay soils. Principal plants include creosote bush (*Larrea divaricata*), tarbush (*Flourensia cernua*), crucifixion thorn (*Koeberlinia spinosa*), mesquite (*Prosopis juliflora*), sumac (*Rhus microphylla*), tabosa grass (*Hilaria mutica*), and narrow-leaf yucca (*Yucca elata*); less prominent are lote bush (*Condalia lycioides*) and tumbleweed (*Salsola* sp.).

The pond at its maximum fill covers an area of approximately one and a half to two acres and in its deepest part is about five feet deep. Seapwillow (*Baccharis* sp.) and Bermuda grass (*Cynodon dactylon*) fringe parts of the pond (Fig. 1 in Webb, 1969). The water is turbid over a soft mud bottom. The green alga *Spirogyra*, the only aquatic plant, seems most abundant in the winter months when the water is deepest and coldest. Some aquatic invertebrates include bloodworms (Tentapedidae larvae); damselfly and dragonfly naiads; adult bugs and beetles and larvae of the families Corixidae, Nepidae, Belostomatidae, Notonectidae, Dytiscidae, and Hydrophilidae; the gastropods *Physa virgata* and *Planorbella tenuis* (identified by Artie L. Metcalf, University of Texas at El Paso); and three phyllopods, two anostracans *Thamnocephalus platyurus* and *Streptocephalus texanus*, and one notostracan *Triops longicaudatus* (identified by Walter G. Moore, Loyola University, New Orleans). The anuran amphibians *Scaphiopus hammondi* and *Bufo debilis* breed in Taylor Well. Transient ducks occasionally visit Taylor Well; those identified include ruddy ducks, gadwalls, and pintails.

The water in the cattle stock pond at Taylor Well is temporary. In June and most of July the pond is usually dry; 9 April 1964 is the earliest and 3 September 1965 the latest date the pond was known to be dry. The period of dryness, however, is variable, and there may be shallow or occasionally deep water throughout the summer. Most rain falls in August and September, often in torrential downpours; however, a heavy rain filled the previously dry pond on 26 May 1964. Water exceeding three feet in depth occurred throughout the year in 1966, owing to torrential rains on 27-28 June and on 2 August.

Water (two to three inches below the surface) and air (shade, three to five feet above ground) temperatures were taken on different occasions. In water exceeding about two feet in depth, bottom temperatures were cooler than those at the surface. Ice about one-half inch thick covered the pond, except along the shoreline, on 10 December 1966 and on 18 January 1964.

Oviposition

Egg deposition ordinarily occurs twice each year—in the fall following the summer-fall rains that fill the pond and in the spring. In the summer the pond is usually dry. The timing and length of the breeding periods depend on the interaction of temperature and rainfall. Rainfall seems to be the prime factor that motivates breeding. Certainly rainfall stimulates breeding in the fall, following the hot summer months when the pond is usually dry. Spring rains also instigate breeding; in the spring of 1964, when the pond was dry in much of April and May, larvae were seined in June following heavy rains that filled the pond (Webb, 1969). The occurrence of gravid females was recorded on 7 March, 7 April, 15 April, 3 June, 9 June, and 1 December. The gravid female obtained on 1 December (both water and air temperature, 12 C) suggests breeding in cold months of winter (Hassinger, Anderson, and Dalrymple, 1970) or that eggs may be retained until spring. During mild winters, egg deposition may be uninterrupted from fall through spring. Eggs were found only twice in the fall—on the same date, 22 September, in 1966 and 1968; water occurred throughout the year in 1966, but torrential rains on 2 August probably stimulated breeding. In spring, eggs were discovered as early as 25 February 1968, and as late as 19 April 1969; however, on both of these dates most embryos were in late stages of development, suggesting that oviposition occurred perhaps a week earlier in each month. Water temperatures recorded on eight occasions when eggs were discovered ranged from 12 to 22 (average, 18) C.

Eggs seem to be deposited on any submerged object. Eggs were most commonly found on scattered twigs and branches, especially on the submerged parts of tumbleweeds that blew into the water (Fig. 2); eggs were also found on cow droppings and the rungs of a barbed wire fence. Eggs were scattered in irregular fashion. A captive female wandered aimlessly and slowly through a tumbleweed bramble, stopping momentarily while depositing eggs; the period of egg deposition lasted about five hours. Eggs were usually deposited singly, often in pairs, and rarely in diffusely arrayed, mostly linear masses of three to nine eggs. Eggs in different stages of development may occur on the same twig or branch. The outermost gelatinous envelope is sticky and clear in recently deposited eggs but with subsequent development the envelope becomes brownish and cloudy owing to the adherence of suspended particles in the turbid pond water.

Fig. 2. Eggs (embryos) of *Ambystoma tigrinum* on tumbleweed (single egg and row of three in center); photograph taken 1 March 1969 by Richard C. Lovelace.

Eggs

Difficulties in interpretation and/or scrutiny of observation coupled with variation of some sort would allow for the discrepancy in the number and relative thickness of the investing egg envelopes or capsules of *Ambystoma tigrinum* to judge from a comparison of our eggs with those depicted in the illustrations by Storer (1925), Smith (1934), Bishop (1941), and Salthe (1963); a seemingly pertinent, but not readily accessible, paper (Wintrebert, 1912) was not consulted.

The fertilized egg, with the closely adpressed fertilization membrane, is surrounded by three gelatinous envelopes or capsules, designated inner, middle, and outer (Fig. 3). The animal pole is

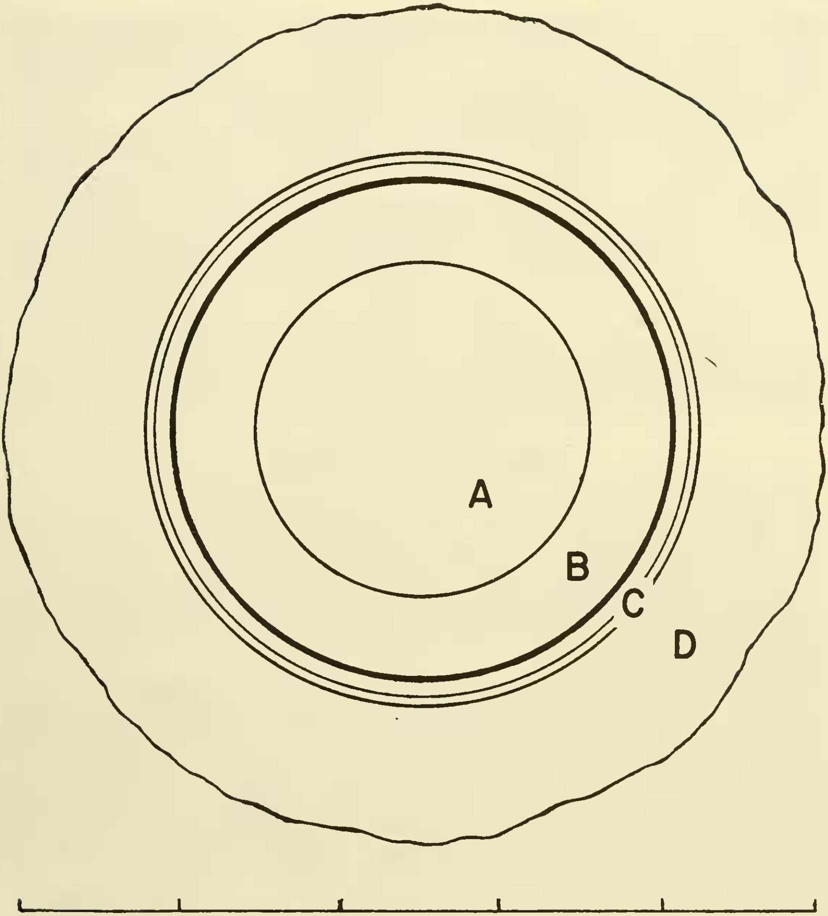

Fig. 3. Diagrammatic sketch of fertilized egg with gelatinous capsules or envelopes. *A*, vitellus (closely adpressed fertilization membrane and pigmentation not shown); *B*, fluid-filled capsular chamber with thin outer restraining capsule (heavy black border); *C*, middle double envelope; *D*, outer envelope. Line equals 5 mm.

pale brown or orange-brown, whereas the vegetal pole is whitish. The inner and middle envelopes are apparently double. The dissolved innermost part of the inner envelope forms a fluid-filled capsular chamber (Salthe, 1963) enclosing the floating egg or vitellus. The restraining boundary of the capsular chamber (enclosing capsular fluid) is a very thin, tough, and elastic capsule. In long preserved eggs (10 percent formalin), the capsular chamber with its outer restraining, thin capsule is often separated in places from the middle envelope. The middle envelope, relatively narrow, is also tough and elastic and is composed of two layers of about equal thickness—an inner, semi-opaque, fibrillar layer and an outer clear layer. The outer envelope has an adhesive surface and forms the common gelatinous cover around two or more eggs.

Forty eggs, excluding envelopes, in various stages of early cleavage (measured to nearest 0.1 mm with ocular micrometer) ranged from 1.9 to 2.4 (average, 2.13) mm in diameter. The capsular chamber (with included vitellus and outer thin capsule) varied from 2.7 to 3.4 (average, 3.06) mm in diameter; the average width of this capsular chamber is about 0.50 mm. The middle (double) envelope (with included vitellus) ranged from 3.1 to 4.0 (average, 3.55) mm in diameter; the average width of this double envelope is about 0.25 mm. The outermost envelope is thickest and somewhat variable in width; in two or more eggs there seems to be no demarcation of this envelope around individual eggs.

Embryonic Development

The term "embryo" is applied to the nonfeeding individual from the time of fertilization until hatching, or when the individual is free of the gelatinous envelopes. To judge from observations of eggs laid by a captive female, most if not all newly deposited eggs show no signs of cleavage. Data are available on variation in time of development at different temperatures in the laboratory and in the pond at Taylor Well.

In the laboratory some embryos (eggs) were reared through hatching in pond water approximating 25 C. Observations of embryos preserved at various time intervals indicate the approximate time span between some developmental stages. The approximate time elapsed since deposition and the corresponding stage of development are: 12 hours—early cleavage, 24 hours—late cleavage, 90 hours—neural tube and tail bud stages, 156 hours—embryos wriggling periodically in envelopes, and 204 hours—hatching. After 156 hours, the wriggling embryos have three pairs of gills; the smallest embryos, about 6 mm long, lack gill fimbriae and have mostly white bodies with few melanophores, whereas the largest embryos, about 8 mm long, have gill fimbriae and prominent black peppering on the sides of the body. The smallest larvae at hatching measure 9 mm. The period of embryonic development is approximately 204 hours (8.5 days) at a temperature of 25 C.

Two sets of embryos (in different stages of development) were discovered at Taylor Well on 19 March 1966 (water temperature, 18 C). The least developed set (outermost envelopes transparent) was judged to be comprised of embryos in the period of cleavage, whereas the somewhat elongated embryos of the other set (partly visible through cloudy outermost envelopes) were near hatching. Embryos representing both developmental stages occurred close together in the same tumbleweed bramble. On 26 March (water temperature, 18 C), some embryos had hatched into larvae, as indicated by spent jelly envelopes. Almost all other embryos had cloudy outer envelopes and were in late stages of development, suggesting that those observed on 19 March in the period of cleavage had developed to near hatching in the seven-day interval. These embryos were wrapped in cheesecloth to trap the larvae after hatching. Almost all embryos had hatched 11 days later on 6 April (water temperature, 15 C). The larvae trapped in cheesecloth averaged 11.8 (9 to 17) mm.

These data suggest an approximate period of embryonic development of 18 days at a temperature of 15 to 18 C, which is about twice as long as that for embryos raised at a temperature of 25 C.

Larvae

The term "larva" refers to the feeding individual having external gills from the time of hatching (free of gelatinous envelopes) until either the gills are resorbed (adults or subadults) or until gilled individuals attain sexual maturity (neotenes).

At hatching, larvae are 9 to 10 (body about 6 and tail 4) mm. Balancers are absent. The head is large with prominent black eyes. Dark pigmentation is lacking ventrally, is sparse ventrolaterally, and is extensive dorsally and dorsolaterally. Consistent pattern features are a middorsal row of unpaired dark blotches alternating with four to six pale blotches (occasionally with scattered melanophores), and a pale postocular spot that is often continuous with a pale dorsolateral stripe on the body (Fig. 4); this pattern is evident in larvae 17 mm long. This dorsal pattern seems to differ from that of paired dorsal dark blotches ascribed to hatchling larvae by Bishop (1941: 164, Fig. 33c) and Brandon (1961:382).

Larvae 22 to 23 mm and at all larger sizes, including neotenes, are generally dark green or olive-green; occasional larvae are pallid, mostly white. Two consistent features of pattern—a black preocular streak and a dark, somewhat diffuse tail tip—become indistinct or

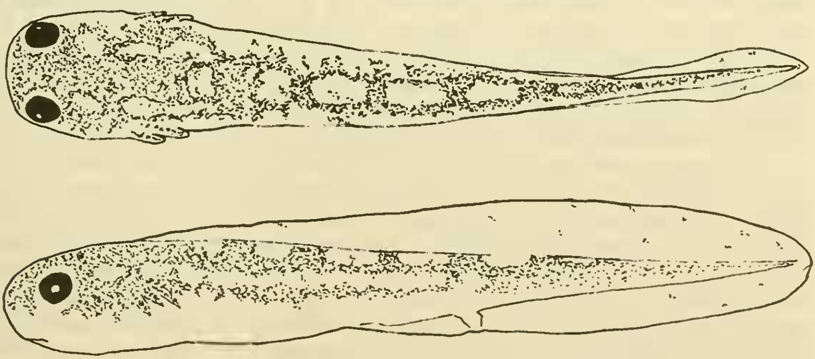

Fig. 4. Dorsal and lateral view of hatchling larva, 9 to 10 mm in total length, of *Ambystoma tigrinum* showing characteristic pattern of pale lateral stripe and middorsal blotches.

absent with increasing size, especially the black tail tip; the black preocular streak may be evident in large neotenes. Contrasting patterns are evident in larvae and presumably signify the advent of transformation (Fig. 9); the pattern seems to develop initially on the tail. Larvae 22 to 23 mm have small forelimbs. Hind limbs were first noticed when larvae were 28 mm; the hind limbs are about 2 mm long when larvae are 36 mm long. Larvae up to a size of at least 110 mm show a bronzish iridescence on parts of the body and often have a row of golden spots on the sides.

Growth of Larvae

The rate of growth was recorded for a few larvae that hatched in the laboratory; conditions were not suitable for continued growth and these larvae eventually died. The temperature varied from 22 to 24 C. Four hatchling larvae increased 2 (from 10 to 12) mm in about two days, whereas three larvae that hatched under the same conditions increased 3 (from 10 to 13) mm in five days. Three larvae, representing a different set of hatchlings, increased 2 (from 15 to 17) mm in about four days, 5 (17 to 22) mm in 12 days, and 6, 8, and 13 (22 to 28, 30, and 35) mm in 12 days.

Data on growth rates were obtained at different times in the years 1964 and 1966 by periodically measuring marked larvae of various sizes that were placed in pens in the pond at Taylor Well. Larvae were marked for individual recognition by clipping digits (no more than one digit per limb). The maximum number of larvae in each pen varied from five to seven. The circular pens of hardware cloth had diameters of 26 inches. Individual growth rates are shown in figure 5. As expected, growth rates of larvae of all sizes were slower in winter (February-March) than in summer (May-September).

In winter, from 15 February to 7 March 1964, 13 larvae ranging from 65 to 152 mm increased an average of only 3.3 mm; the water temperature ranged from 9 (February) to 14 (March) C. Some of these larvae showed no increase in length. Of these 13 larvae, six increased from extremes of 110 and 152 to 112 and 155 mm, showing an average increment of growth of 2.5 (0 to 5) mm; seven smaller larvae increased from extremes of 65 and 90 to 66 and 94 mm, showing a slightly higher average increment of 4.0 (0 to 8) mm.

In summer and early fall (17 May through 21 September), 13 larvae ranging from 48 to 100 mm increased an average of 15.1 (9 to 18) mm; water temperatures ranged from 20 to 30 C. From 17 May to 5 June 1966 (water temperatures 25 and 30 C, respectively), two larvae 98 and 100 mm increased to 115 and 118 mm, respectively, an average increase of 17.5 mm; in this same time period a small larva 48 mm long increased 13 mm to 61 mm (not depicted in Fig. 5). From 3 July (water temperature not recorded) to 10 August 1964 (water temperature, 26 C), five larvae increased from extremes of 86 and 95 to 97 and 110 mm, showing an average growth increment of 14.2 (9 to 18) mm. From 27 August to 21 September 1964 (water temperatures 20 and 23 C, respectively),

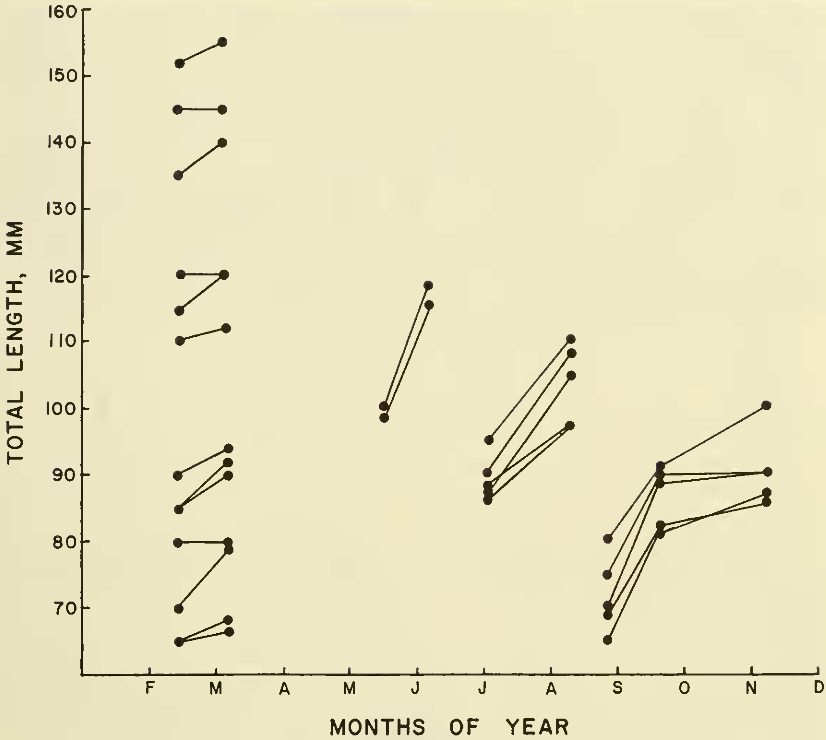

Fig. 5. Growth rates of individual salamanders of different sizes in different months of different years (see text).

five larvae increased from extremes of 65 and 80 to 82 and 92 mm, showing an average increase of 15.4 (12 to 18) mm.

Also depicted in figure 5 is a retardation in growth rate (from 21 September to 8 November 1964) of the five larvae that grew rapidly from 27 August to 21 September. These larvae increased to extremes of 86 and 100 mm by 8 November, showing an average increase of only 3.4 (0 to 8) mm. The water temperature on 8 November was 16 C. Four of the five larvae had gill stubs, indicating transformation; these larvae increased 0, 1, 3, and 5 mm, whereas the one gilled larva increased 8 mm. Although the low temperature may have been a factor, the slow rate of growth is attributed to the physiology of transformation.

Seine samples in 1966 provide data on the collective growth rate of larvae hatched in the spring of that year. The pond at Taylor Well was dry in the summer of 1965. Following heavy rains, seining operations revealed no salamanders either in the fall of 1965 or in the winter months of 1966. Perhaps bulldozing activities to enlarge the pond in the summer of 1965, and a torrential four-inch rain on 4 September that caused mild flooding, contributed to disrupt the fall breeding pattern. On 19 March 1966 no larvae were found after a diligent seining operation, but embryos (eggs) were extremely abundant. Some of these embryos were in late stages of development and hatched sometime prior to 26 March, whereas other embryos in early stages of development hatched about 6 April (see section on embryonic development for further data). It is assumed that egg deposition did not occur in the fall of 1965 and that these hatchling larvae were the only larvae in the pond. Although the four seine samples on 17 May, 5 June, 4 July, and 16 August do not indicate all sizes or size extremes, the general trend of growth of larvae is probably adequately expressed by the histograms shown in figure 6.

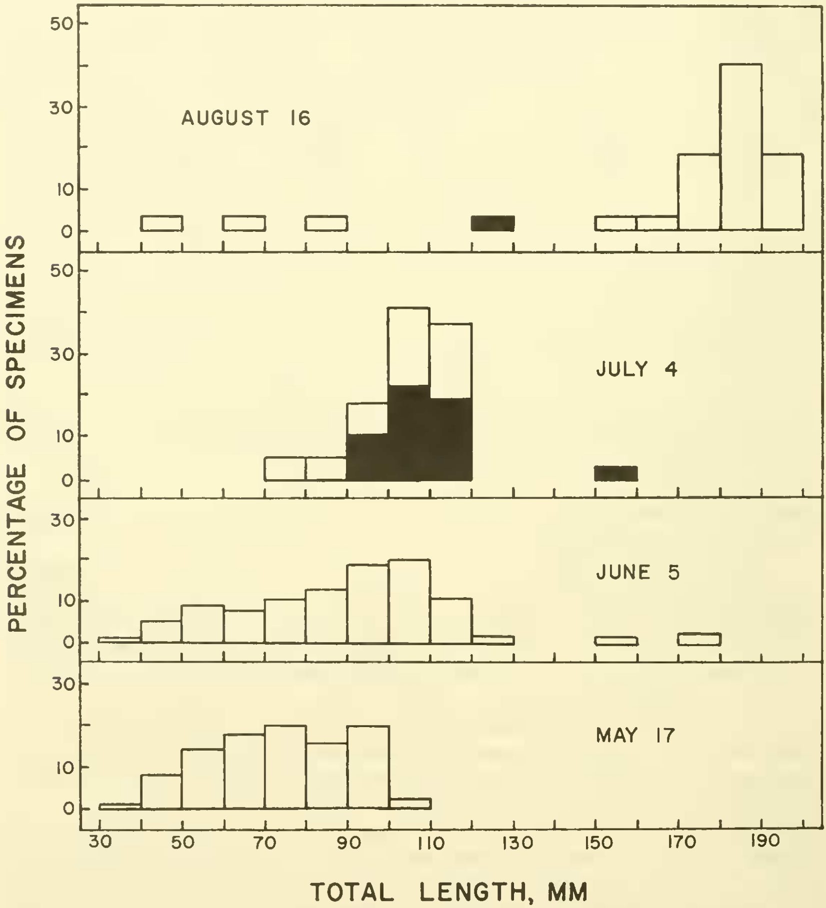

Fig. 6. General growth trend of larvae hatched in interval 23 March to 6 April 1966 in months of May, June, July, and August; solid parts of bars indicate subadults (see text).

On 17 May, larvae ranged from 39 to 101 mm; most larvae (74 percent) ranged from 61 to 100, averaging 81.6 mm. On 5 June, after a lapse of 18 days, larvae ranged from 38 to 176 mm (only three larvae, 155, 174, and 176, exceeding 122 mm); most larvae (74 percent) ranged from 71 to 117, averaging 97.0 mm. The average increment of increase for most larvae (74 percent of each sample) was 15.4 mm, which is about the same rate of growth recorded for individually marked larvae observed in pens in the same time interval. Presumably, some larvae are capable of growing to a length of 176 mm in about 74 days (23 March to 5 June).

About one month later, on 4 July, the sample of salamanders contained about equal numbers of larvae and transformed subadults. Previously, however, in the period 5 June through 11 June, many larvae were subjected to stress when they were trapped by the receding water level in an isolated, drying, shallow pool; some of these trapped salamanders (six of the largest, 103 to 118, averaged 106.8 mm) were transforming to subadults as evidenced by short gill stubs (none were preserved; see section on transformation for further data). Water in the adjacent large pond averaged some three feet in depth. Later, on 27-28 June, heavy rains (approximately 1.5 inches in two hours in El Paso) filled the pond so that subsequent seining operations were difficult and confined to the periphery of the pond. The sample obtained on 4 July included salamanders ranging in total length from 75 to 120 mm, except for one transformed individual of 155 mm. Most salamanders (87 percent) ranged from 95 to 120 mm; of these, however, over half (55 percent) were transformed subadults. These subadult salamanders averaged 107.0 (97 to 120) mm and seemed to represent those larvae that moved overland to the large pond after transformation under stress. Some larvae in the large pond, however, may have transformed in the absence of stress conditions. Most larvae (those included with the subadults, 87 percent) also averaged 107.0 (95 to 114) mm in total length. The average increment of increase for these larvae since 5 June was 10.0 mm. Since growth is retarded during transformation, the average size of the larvae would be expected to be larger than that of the subadults. This lack of larger larvae is perhaps due to the difficulty in obtaining an adequate sample because of the deep water. That the bulk of the larvae in the July sample should be larger than is indicated in figure 6 is suggested by the general maximum size-frequency trend in growth noted in the adjacent months.

On 16 August the pond was still near maximum depth, owing to another torrential downpour on 2 August (approximately two inches in one hour that caused minor flooding in El Paso). Larvae ranged from 43 to 198 mm. Most larvae (79 percent) ranged from 175 to 198, averaging 185.6 mm. The average increment of increase for these larvae since 4 July was 78.6 mm in 43 days or 1.8 mm each day; this rate of growth is excessive, since the bulk of larvae in the July sample should probably average larger in size. However, rapid growth might be expected, owing to the latent influence of the heavy rains on 2 August that enlarged the pond to provide less crowded conditions and more nutriments. The small larvae presumably represent those of arrested development or late hatchlings since no eggs or spent gelatinous envelopes could be found after a diligent search.

On 22 September a few embryos in late stages of development were discovered, as well as one sexually mature male (180 mm long) with small gill stubs (recently transformed). A sample obtained on 30 September using a larger seine (12 foot) than that used previously (6 foot) yielded few salamanders after many hauls; the full pond was difficult to seine. One subadult measured 157 mm, and two sexually mature males measured 210 and 213 (smallest recently transformed with gill stubs about 3 mm long); four larvae ranged from 210 to 220, and two smaller larvae were 195 and 100 mm. The four large larvae averaged 215.8 mm, indicating an average increment of increase of 30.2 mm since 16 August.

The next seine sample taken the following year on 15 April 1967, when the water level had receded considerably, yielded larvae ranging from 47 to 233 mm, subadults from 160 to 180, transformed mature males from 195 to 236 mm, and four neotenic individuals—two males of 245 and 260 mm, and two females of 246 and 252 mm. The largest larvae doubtless represent those hatched from eggs deposited in the spring of 1966. The eight largest larvae (including the four neotenes) averaged 240.1 (225 to 260) mm, showing an average increase since 30 September of 24.3 mm. The sample obtained on 15 April 1967 was the first since operations began in September of 1962 that contained neotenic individuals. Also, 1966 was the first year since this study began that the pond was known to have had water at least three feet deep throughout the year.

The data suggest that growth rates are variable, with higher temperatures and probably lower population densities providing for the most rapid increments of increase. Growth rates seem to be slowed during transformation. Individual larvae attained a size of 260 mm after a period of about 388 days (23 March 1966 to 15 April 1967); this size-time correlation agrees with data provided by Glass (1951). Permanent water tends to promote neoteny.

Transformation

Individuals that transform prior to attaining sexual maturity are referred to as subadults, whereas sexually mature transformed individuals are referred to as adults. Larvae in the pond at Taylor Well have the capacity to transform at varying sizes exceeding about 90 mm. Most, if not all, of the smallest subadults probably transform under conditions of stress. The smallest subadult measured 88 mm at the time of complete transformation but, after a few years of preservation, now measures 82 mm (Fig. 9). Some larvae transform spontaneously (no apparent stress conditions), whereas others fail to transform and become sexually mature or neotenic. Obligate neotenes are unknown. Knopf (1962) noted metamorphic variation among individuals from the same lake in the Texas Panhandle.

Under natural conditions, drying of habitat in late spring and early summer causes transformation (Webb, 1969; Gehlbach, 1965). On 5 June 1966 a small pool, isolated some 15 feet from the large pond, contained about three inches of water (temperature 30 C in late afternoon). None of the larvae in this pool exceeded 120 mm. On 8 June evaporation had confined water to several shallow puddles interconnected by wet mud. Several desiccated, small larvae, 40 to 60 mm, were imbedded in the drying mud. The water in the shallow puddles was one to three inches in depth where the tail fin or back of the largest larvae was often exposed. Many of the largest larvae were in the process of transformation and had only gill stubs; six of them averaged 106.8, ranging from 103 to 118 mm. In bright sun from 3:00 to 4:45 p.m. (air temperature 35 C), two salamanders were observed to move from puddle to puddle over the wet mud. Three days later in the afternoon of 11 June, only two small depressions of wet mud with wriggling, air-gulping, mud-caked larvae remained. These gilled larvae showed no signs of transformation (the three largest measured 80, 85, and 90 mm) and undoubtedly died. The majority of these larvae, whose growth had been traced since hatching, transformed after a period of approximately 78 days (23 March to 9 June; Webb, 1969). After transformation, subadults return to water, if available; the food of subadults indicates an aquatic habit (see section on food). If water is not available, salamanders presumably take refuge in rodent burrows; Hamilton (1946) noted their occurrence in this retreat in summer in central New Mexico.

Larvae may transform without desiccation of habitat, which is the usual developmental pattern for *Ambystoma tigrinum* in the eastern United States (Brandon and Bremer, 1967). Recently transformed males bearing small gill stubs have been seined from deep cold water (22 and 30 September 1966).

Some small larvae, about 40 to 50 mm, that were seined from the pond at Taylor Well on 2 February 1963 were placed in an aerated aquarium containing tap water about one foot deep with a relatively constant temperature near 25 C. The larvae were fed bits of liver and showed variable growth through March. In April, complete transformation of eight larvae occurred at the following sizes (and dates): 7 April—100 mm; 10 April—105; 11 April—88; 12 April—105; 13 April—103; 14 April—91 and 105; and 19 April—97 mm. These larvae, 88 to 105, averaged 99.3 mm. One larva that grew much faster than the other larvae was transferred to another aquarium because of its cannibalistic tendencies; this large larva in tap water at the same temperature transformed on 23 April at a size of 131 mm. Two slow-growing larvae showed no signs of transformation on 4 May at sizes of 76 and 85 mm. Thirteen large larvae showing no signs of transformation were seined on 16 August 1966 (water temperature not recorded) and were transferred to tap water (about 25 C) in the laboratory; all larvae were completely transformed by 31 August and averaged 176.0 (165 to 185) mm. The water temperature, relatively higher than at Taylor Well, rather than the chemistry of the tap water probably prompted transformation.

There is some further evidence that cold water prevents transformation. Three dark brown, patternless, similar-sized larvae obtained from a permanent coldwater (relatively constant near 10 C), dimly illuminated, rocky pothole in a small cave in the Hueco Mountains east of El Paso demonstrated varying degrees of transformation in the laboratory. None transformed in room-temperature tap water. Two transformed when thyroxine tablets were added to the water (concentration unknown); the third larva, a neotenic female 185 mm long, failed to transform after corresponding thyroxine treatment and showed only shriveled gills after prolonged living in warm, room-temperature tap water. Three neotenes were received from Mr. Bob Frampton (Alamagordo, New Mexico) who raises "waterdogs" for commercial purposes. These neotenes measured 305 (female) and 298 and 310 (males) mm and were raised and received from Frampton in clear, cold water (temperature unknown); when transferred to warmer tap water (about 25 C) the three neotenes transformed.

Individual larvae seem to respond differently to the same stress conditions. In a sense, the term "environmental stress" is relative; the usual wet-dry annual cycle, in which larvae transform at varying sizes, can be considered as providing more "stress" than the continuous wet cycle in which water is continuous throughout the year and there is selection for neotenes.

The exact factors responsible for transformation are unknown. Gehlbach's observations (1965) that increased temperatures and decreased oxygen supply associated with drying of habitat promote transformation agree with our observations. Our data also support the comments of Smith (1969) and Wintrebert (1907) that the limits of individual variation in the capacity to transform are genetically determined but modified by environmental conditions.

Size at Sexual Maturity

Sexual maturity of all salamanders was determined by dissection. Rodgers and Risley (1938) and Baker and Taylor (1964) have described the morphology of the urogenital system of *Ambystoma tigrinum*. Our criteria for sexual maturity are a swollen and convoluted Wolffian duct in males and oviduct in females; these ducts are straight and narrow in immature salamanders. Rodgers and Risley (1938) have shown that the development of Wolffian ducts is correlated with the appearance of spermatocytes, and of oviducts, with the growth of ovocytes. In sexually mature males, cloacal lips are black and swollen. Some females having oviducts only slightly swollen and convoluted, suggesting the onset of sexual maturity, are referred to as submature in figure 7.

Transformed individuals of both sexes are sexually mature at a smaller size than neotenes, and there seem to be no sexual differences in size at sexual maturity (Fig. 7). Data, however, are scanty for

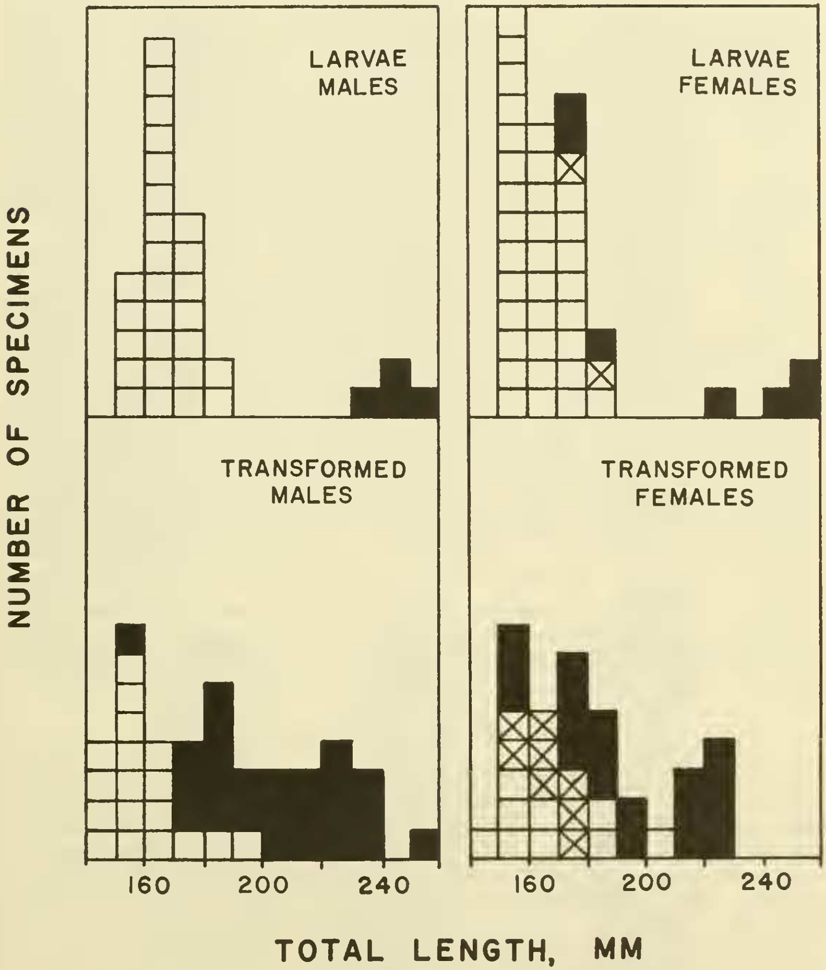

Fig. 7. Size at sexual maturity in males and females of larvae (neotenes) and transformed individuals; open squares, immature; diagonal-marked squares, submature; solid squares, sexually mature. Each square represents one individual.

neotenes, especially males. Our sample of 25 transformed adult males averages 204.4 (156 to 256) mm, and of 19 transformed adult females averages 190.5 (154 to 222) mm. Corresponding data for neotenic males are lacking (four measure 236, 240, 245, and 260 mm), but the advent of sexual maturity seems to occur at a larger size than in transformed males. Seven neotenic females average 215.9 (172 to 255) mm.

If larvae smaller than 150 mm transform, they will be subadults. If larvae exceeding 150 mm transform, they will be adults either at transformation or shortly thereafter. Two sexually mature salamanders seined at Taylor Well measured 180 and 210 mm and had recently transformed, as evidenced by short gill stubs. Transformation under stress may delay the onset of sexual maturity. Thirteen larvae induced to transform in tap water in the laboratory showed no signs of sexual maturity after complete transformation on 31 August when they averaged 176.0 (165 to 185) mm; about one month later on 1 October and after a slight increase in length, the males, ranging from 175 to 190 mm, showed partially swollen and black-edged cloacal lips and the onset of sexual maturity.

Assuming 150 mm as the smallest size at sexual maturity in both sexes of transformed salamanders and 170 mm in both sexes of neotenes, the data on growth of larvae suggest that sexual maturity may be attained after a period of development of only 74 days or about 2½ months (23 March to 5 June 1966; hatching known to have occurred in interval 20-26 March). Most larvae are capable of becoming sexually mature after a period of 146 days or about five months (23 March to 16 August 1966), when an average size of 185.6 mm is attained; the size minimum for sexual maturity in most of these salamanders is probably attained in about four months. The period of larval development is doubtless variable depending on the time of hatching and the permanency and amount of water. We have no data on growth rates of neotenes and transformed individuals. If both morphotypes hatch at about the same time, larger neotenes are probably of about the same age as smaller transformed individuals, since growth seems to be retarded during transformation.

Subadults and Adults

The color and pattern of transformed salamanders is variable and depends largely on the size at transformation. Most of the smallest subadults (near 100 mm) are a uniform dark olive green or brown with only an obscure and diffuse mottled and blotched pattern; but some of them (as small as 94 mm) may show contrasting patterns (Fig. 8). The contrasting pattern, then, is not correlated with the advent of sexual maturity. The mostly patternless subadults undergo ontogenetic change and acquire a contrasting pattern with increasing size; the degree of ontogenetic variation in transformed salamanders (Gehlbach, 1965) has not been studied. Contrasting patterns are evident in larvae presumably just prior to transformation (Fig. 9). Two extreme pattern-types of adults are (1) ground color mostly black with pale yellow markings and (2) the reverse of that pattern, with the ground color mostly pale yellow with few black markings. Pattern type 1 is most common, but patterns intermediate between the two types occur. Often the ground color is olive or brownish so that patterns are noncontrasting.

Food

Data on kinds of food consumed is scanty. Food capture is probably triggered primarily by movement. The carnivorous diet of tiger

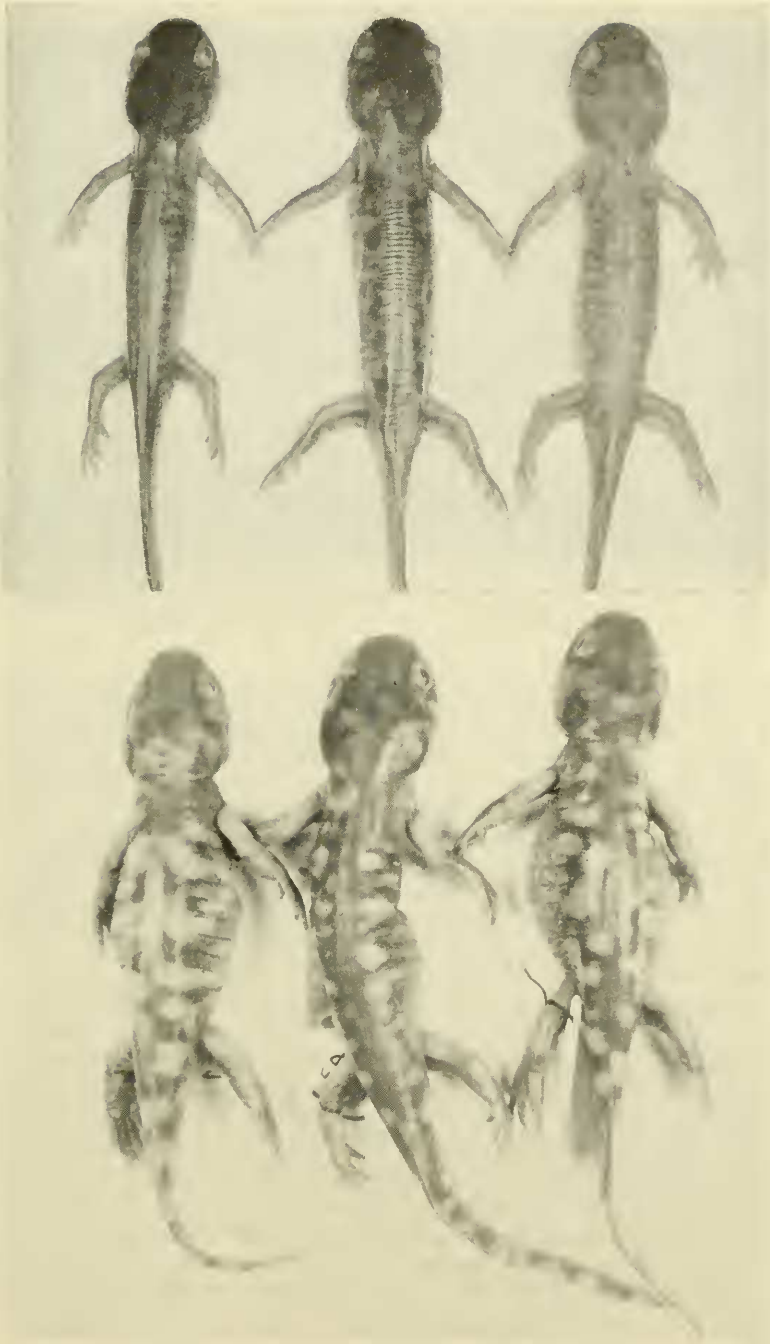

Fig. 8. Variation in pattern of subadult *Ambystoma tigrinum* that transformed under stress. Top, mostly patternless; left to right, 82, 91, and 95 mm total length. Bottom, distinctly patterned; left to right, 94, 107, and 100 mm total length; photograph by Rayburn Ray.

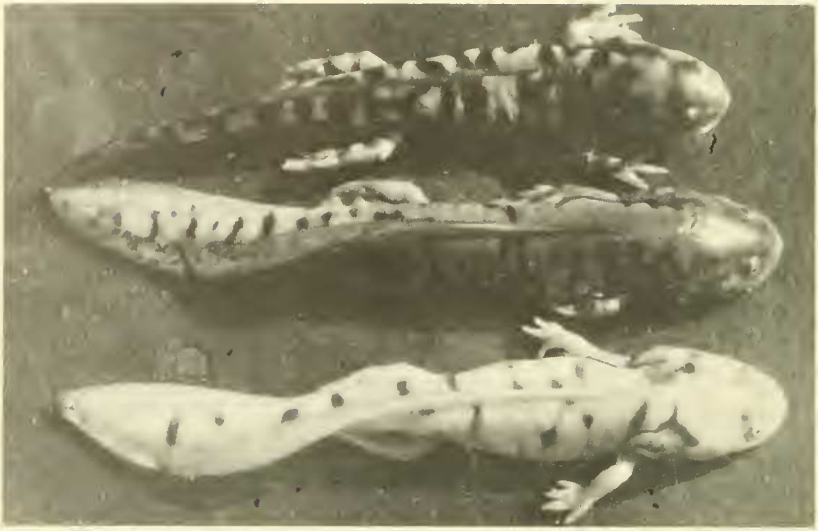

Fig. 9. Variation in pattern of *Ambystoma tigrinum* larvae just prior to transformation; top to bottom, 160, 168, and 160 mm total length.

salamanders and the cannibalism of larvae is well known. Cannibalism was frequently observed among captive larvae less than 100 mm long. The larvae constantly nip at each other. Individuals may be ingested either head or tail first. The size discrepancy between predator and prey must be about 15 to 20 mm, otherwise the prey larva, usually only partly ingested and killed, is regurgitated. Beetle elytra and mud balls held together by strands of *Spirogyra* were either defecated or observed in stomachs of large larvae and recently transformed individuals in the size-range 150 to 170 mm. Captive adults and subadults ate insects, including grasshoppers, cockroaches, crickets, houseflies, june bugs, and moths, and at times were observed to ingest parts of their shed epidermis.

Food items in stomachs of 13 subadults, 90 to 120 mm long (collected 3 February 1968) included insects (identified by James R. Zimmerman, New Mexico State University) and tadpoles of *Scaphiopus*, indicating an aquatic habit and ingestion of nonaquatic insects that fall to the surface of the water. Little and Keller (1937) also recorded these same food items for salamanders from the Jornada range headquarters about six miles north of Taylor Well. Tadpoles of *Scaphiopus* were most frequent. The frequency of occurrence (number of individuals/number of stomachs) for each food item is as follows: Spadefoot toad (*Scaphiopus*) tadpoles, bodies 7-8 mm long, 130/13; Orthoptera, 1/1; Isoptera (winged), 34/10; Corixidae, 1/1; Coleoptera, unidentified fragment, 1/1; Hydrophilidae (*Berosus*), 1/1; Formicidae, 11/6.

Mortality

Although evidence is lacking, cannibalism probably occurs among larvae at Taylor Well, and some larvae probably fall prey to the predaceous larvae or adults of aquatic insects. Many small-sized larvae desiccate when the pond dries in summer. Transformed individuals that seek refuge in the mud cracks after all water has evaporated can live probably for only a short time; Webb (1969) found one desiccated individual during limited excavation.

There is evidence that larvae or subadults exposed in drying pools of shallow water or shortly after being exposed are preyed upon by coyotes. A person (name unknown) knowledgeable concerning the upkeep of Taylor Well visited briefly with Webb on 17 April 1964 when he was digging and searching for salamanders in the mud cracks. This person said that when the pond was mostly dry with scattered soft mud depressions on 7 April, many larvae were thrashing in the mud or had desiccated; he also pointed out impressions of coyote tracks and scratchings in the mud and said that coyotes, as well as bobcats, eat the salamanders. That coyotes frequent Taylor Well is evidenced by the discovery of two dead coyotes (seemingly poisoned) found along the south shoreline on 1 March 1969.

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